

**Asexual reproduction in *Linuche unguiculata* (Swartz, 1788)
(Scyphozoa: Coronatae) by planuloid formation through
strobilation and segmentation**

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Abstract.—Scyphistomae of *Linuche unguiculata* from São Paulo State, Brazil, were reared for one year to study the life cycle of this warm-water species (in subtropical western South Atlantic waters). We found *L. unguiculata* reproduces more by the development of planuloids than by medusae. The scyphistoma is rejuvenated by an operculated regression-regeneration cycle. We hypothesize that reproduction of the species by production, either via segmentation or strobilation, and liberation of planuloids explains the absence of reports of ephyrae and medusae in the area.

Jarms (1997) reviewed the history of knowledge about scyphistomae of Coronatae. The only records of coronate Scyphozoa from the Brazilian coast are of the medusa stage of *Nausithoe punctata* Kölliker, 1853, from the north of Bahia State (Goy 1979) and material recorded during study of the life cycle of *Nausithoe aurea* Silveira & Morandini, 1997, from the north of São Paulo State. Silveira & Morandini (1996) redescribed the scyphistoma of a coronate, *Stephanoscyphistoma corniformis* (Komai, 1936), from the south-east Brazilian coast. The present study on the life cycle of *L. unguiculata* was undertaken over a 14 month interval. Observations were based on cultures of the scyphistomae from south-east Brazil.

We found colonial coronate scyphistomae (presumed to be *L. unguiculata*) frequently in São Sebastião Channel, and we asked: why are there no records of medusae or of any dermatitis caused by their planulae? We presumed three possible explanations to account for this: the ephyrae belong to suprabenthic communities and are transported to distant places, so that medusae of this species are not found near the coast; *L.*

unguiculata typically passes intervals of many years between periods of production of large numbers of medusae (Russell & Tomchik 1993, Black et al. 1994); therefore it would not be strange that between these periods the probability of finding medusae were very small; the species was not *L. unguiculata*, although the characters of the periderm tubes of our material were similar to that reported in the species.

Our field observations were that no ephyrae/medusae occurred in plankton or suprabenthic samples during 1 yr and our laboratory observations were that few polyps strobilated producing a small number of ephyrae, but many planuloids were produced together with segmentation of other scyphistomae. Thus, few ephyrae were produced, which supports the second explanation.

Material and Methods

Colonial scyphistomae (Fig. 1) were sampled from calcareous debris, mainly fragments of the stony coral *Mussismilia hispida* (Verrill, 1902) (Scleractinia, Mussidae) at 2–6 m depth by SCUBA diving, in São Sebastião Channel (23°50'S,

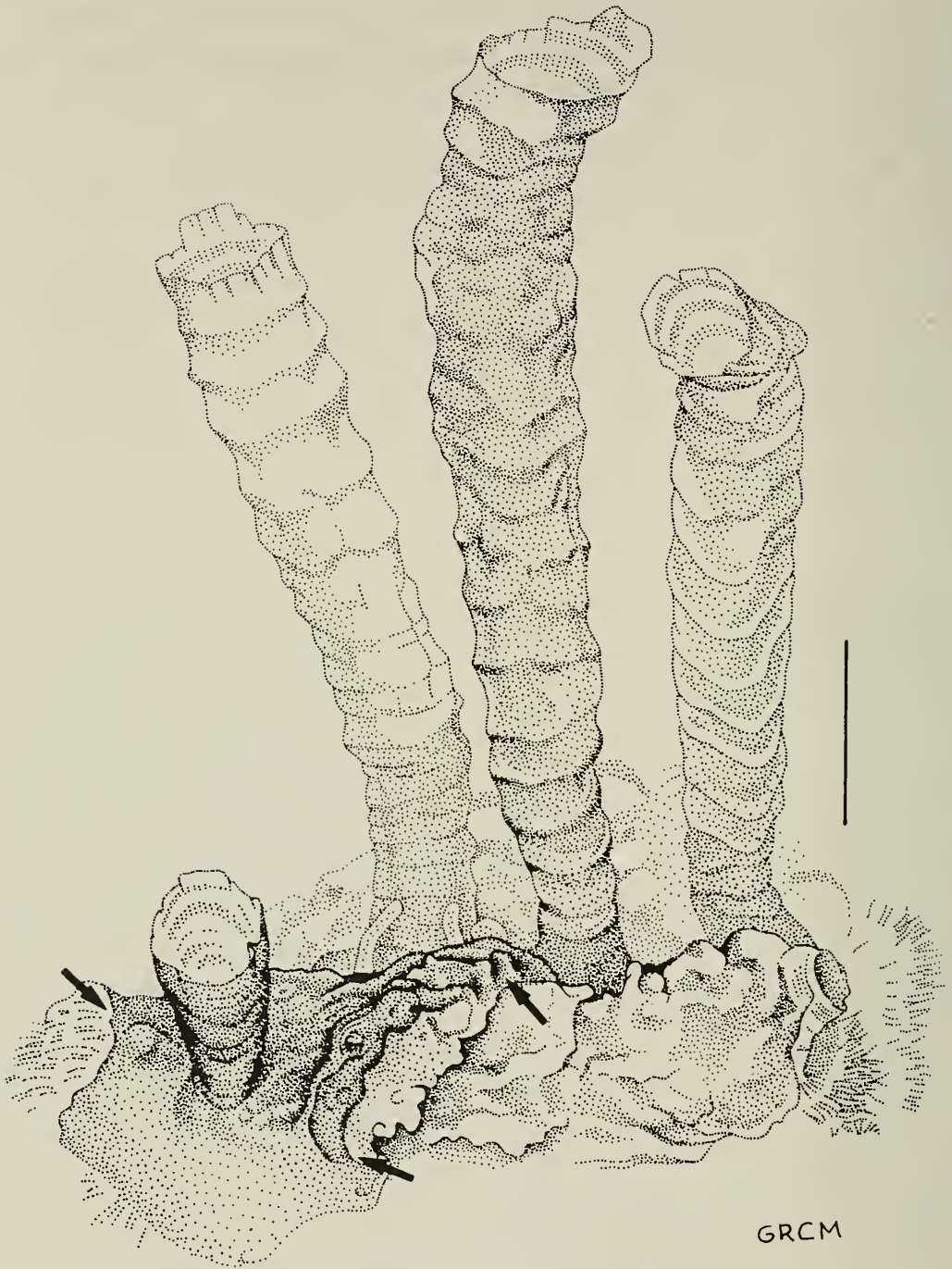


Fig. 1. Colony of *Linuche unguiculata*, as seen soon after sampling. The living tissues are much contracted within the base of the tubes. Note that the scyphorhiza (arrows) is delicate and encrusting. Scale: 0.6 mm.



Fig. 2. Colony of *Linuche unguiculata*. The oral discs of the scyphistomae are partly or fully extended. Scale: 1.25 mm.

45°25'W), of the rocky shore at Urubu Point and on Praia Grande reef, Ilhabela County, SP. Sampling was done on one or two days of every month, except August, from June 1996 until May 1997. We searched for the colonies on lumps of the calcareous substratum collected, with the aid of a stereomicroscope. Each monthly sample included a minimum of 15 colonies,

each with 2 to 8 living polyps (Fig. 2). The colonies were transferred into and maintained in small Petri dishes containing about 70 ml of filtered sea-water. At least twice a month, the colonies were cleaned by gentle rubbing with a delicate brush or by removing the many filamentous algae with fine forceps.

In each search for medusae or ephyrae,

three plankton and suprabenthic faunal samples were taken on three consecutive days following the sampling of calcareous debris. Twenty-minute tows were made in the vicinity of the sampling sites of the debris with a plankton net and a dredge (the last equipment according to Wakabara et al. 1993) at a depth of 5 to 10 m, both with 0.5 mm stretch mesh, using a small outboard motor boat. Two divers followed the equipment to maintain the plankton net at 3 m below the surface and to prevent the dredge from being clogged with bottom sediments.

The scyphistomae reared in the Centro de Biologia Marinha da Universidade de São Paulo (CEBIMar USP), at São Sebastião, SP, were treated as follows. From 6 June to 25 July 1996 all colonies were kept at room temperature (18°C–28°C) and from 1 April to 7 June 1997 half were kept at room temperature (21°C–30°C, although during 24 h the temperature range never exceeded 4°C) and one-half were treated with temperature changes, 18–27–18°C (based on the monthly averages of surface water temperature for winter and summer in the area), at 7-day intervals and $\frac{1}{23}$ h light/dark regime inside an incubator (FANEM® 347-CDG). The scyphistomae reared in the Zoology Department (IB, USP), at São Paulo, SP, were treated as follows. From 26 July 1996 to 11 June 1997 the June–February samples were kept at controlled temperature (August–mid February a monthly increase of 1°C starting at 21°C; mid February–June, a monthly decrease of 1°C starting at 26°C—following the natural surface water temperature monthly averages) and $\frac{6}{18}$ h light/dark regime inside an incubator. The sea water was changed and the animals were fed every other day with a deep-frozen stock of homogenate of the clam *Perna perna* (Linnaeus, 1767) (Bivalvia, Mytilidae). Some of the specimens collected in April 1997 were used to measure the periderm tube (total length, diameter at aperture and base), and the internal cusp was examined in 42 polyps.

Free-swimming ephyrae, from strobilating scyphistomae, were transferred into single airtight pots (universal samplers for medical analysis ZESTER® 140 ml). They were fed from a deep-frozen stock of homogenized clam gonads. The ephyrae and medusa were fed every day. They were individually immersed in the homogenized food, observed under a stereomicroscope until their stomachs were full, and removed to a new pot with clean filtered sea water.

Free-swimming planuloids (samples of March, April and May 1997), produced by strobilating or from segmenting scyphistomae, were transferred into single dishes, at 24 h intervals, for further observations.

We studied the cnidome of live specimens and of specimens preserved in seawater-formaldehyde solution. In preserved tissues, only undischarged nematocysts were measured.

Voucher specimens are: National Museum of Natural History, Smithsonian Institution (USNM 99376, 99377); Museu de Zoologia da Universidade de São Paulo, Brazil (MZUSP 12.355, 12.356); Museu Nacional Universidade Federal do Rio de Janeiro, Brazil (MNRJ 3126, 3127, 3128); The Royal Ontario Museum, Canada, Invertebrate Zoology (ROMIZ B3010, B3011); The Zoologisch Museum, University of Amsterdam, The Netherlands, (ZMA Coel. 8507, 8508); Zoölogisches Museum, Universität Hamburg, Germany, (ZMH C11639, C11640, C11641); and The Natural History Museum, United Kingdom, (NHM 1998.145, 1998.146).

Results

We found no ephyrae or medusae of *Linuchoe unguiculata* in plankton and suprabenthic samples. During June 1996–June 1997, over 240 scyphistomae were reared in the Zoology Department, at São Paulo City, but none of them strobilated. Nevertheless, on many occasions we observed that some scyphistomae produced a periderm operculum closing the tube. The oral

disc and the gastric septa of those scyphistomae regressed, but the column remained and they were able to contract and extend within the tube. We followed some closed tubes over a varied period of 1–3 d, at the end of which the operculum opened and the polyp regenerated septa and the oral disc.

During the period late March–June 1997, among 559 scyphistomae (some 130 colonies) reared at room temperature in CEBI-Mar, only 6 strobilated (two in the same colony) and 3 segmented irregularly.

At the start of strobilation, the polyp resorbed the oral disc, the strobilating region occurred over most of the column, disc number varied from 8 to 17, and no operculum, of either periderm or tissue was present. Initially, the discs were set well apart and the remaining column tissues between them were bulged. From a few hours to 3 d, the discs changed into irregular tissue fragments and most of the remaining and interconnecting column tissues constricted. Only the distal disc enlarged and metamorphosed into an ephyra (Fig. 3), while the other discs directly transformed into planuloids. Among the six strobilae, five released one ephyra each and in another the ephyra transformed into a planuloid within the tube. Release of the ephyra (Fig. 4) varied from 1 to 3 d after onset of strobilation (Table 1). The earliest stage at which the ephyra acquired noticeably medusa-like characters was at about 5 mm in diameter (specimen 8, Table 1). The gonad primordia were four pairs of radiating tissue cords on each side of the perradii. At about 47 d, each gonad pair had fused giving rise to four cleft crescents (Fig. 5). This medusa had an anomalous number of lappets due to an injury at early ephyra stage (fourteen lappets, two perradial pairs being fused, Fig. 5). Most of the zooxanthellae were irregularly distributed within the gastrodermis, in side view mostly below the coronal groove (Fig. 5) and in the corners of the lips of the manubrium. The lappets were round, and slightly overlapping in an orderly fashion, which made the medusa ro-

tate clockwise upon its oral-aboral axis while swimming. The short, translucent tentacles were situated within the clefts between the lappets. The eight conspicuous rhopalia were directed outward while the medusa was at rest or downward during contraction of the bell. The ephyrae of the remaining material were preserved before reaching the medusa stage (Table 1).

At the start of segmentation, the polyp resorbed the oral disc and produced a periderm operculum, it acquired a transverse segmenting region over most of the column, and the segments tended to become spherical in shape. In one colony we observed that in one operculate scyphistoma many planuloids appeared by irregular segmentation. These fused together to restore the column of the polyp, but without differentiation of septa and oral disc (see sequence in Figs. 6, 7). Thus, the process lasted until the end of April. In some colonies, we noted that after a few weeks, near the operculum margin, a fissure developed through which a few planuloids could emerge (Fig. 8). The crack was apparently caused by the egress of the planuloids.

The measurements, length of the tubes and diameter at the base and at the aperture, are: 1.8–12.7 mm, 0.12–0.49 and 0.25–0.68 mm. Most tubes had one cusp; none, two or three were less frequent. The cusps were cup-shaped, with longitudinal ridges, mainly at the broad round margin (Fig. 9). The axis of the cusp base outline was long, narrow, and parallel with the long axis of the tube, whereas the proximal end was bulging and circular (Fig. 9).

Liberated planuloids were elliptical, swam actively by cilia, and had transparent epidermis and a gastrodermis with many zooxanthellae. Two planuloids (from specimen 8, Table 1) settled on the bottom of a small Petri dish on 27 May and 01 June respectively and were reared for 58 and 54 d. Each zooxanthellate polyp had five tentacles within 3 d. Each produced a delicate cylindrical tube, without branching and without cusps.

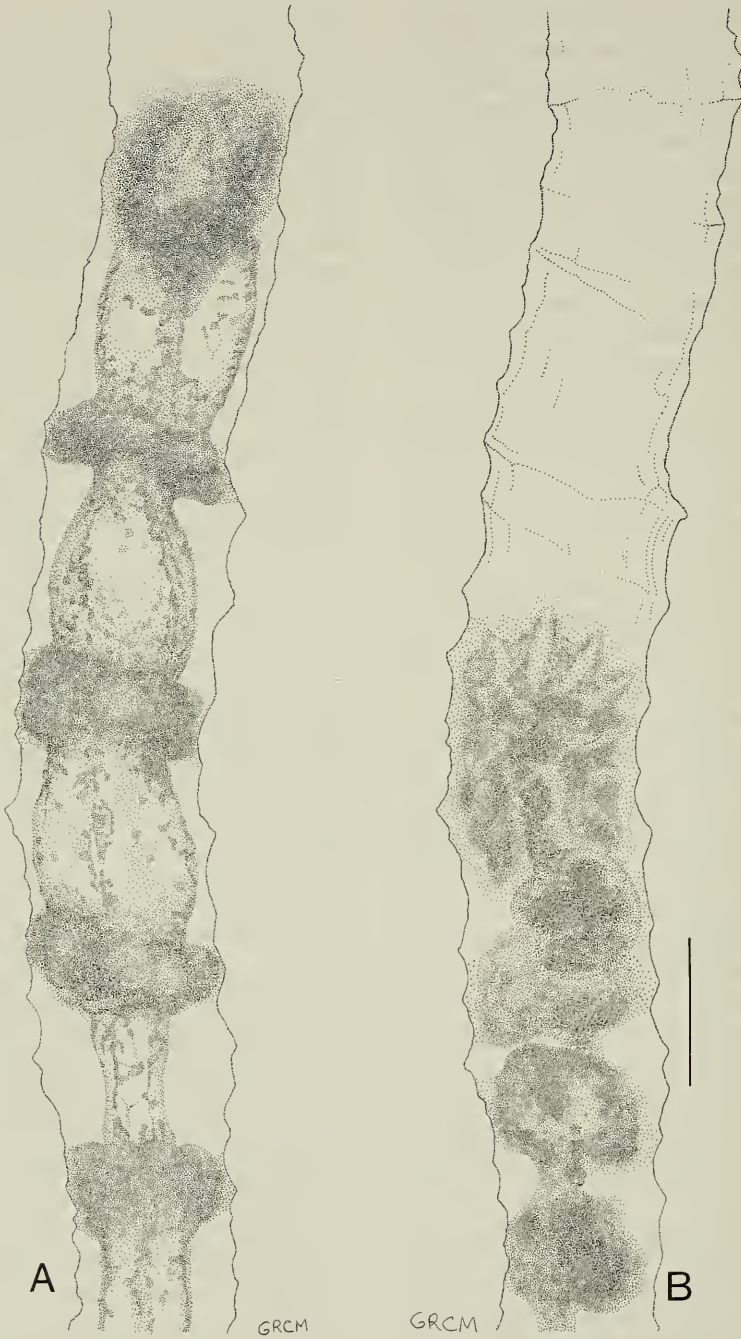


Fig. 3. Strobila of *Linuche unguiculata* (April 1997). A, early strobilation phase, at 24 h, in which the connections between the discs narrow and the distal disc is bigger; B, late strobilation phase, at 72 h, in which the distal disc has differentiated into an ephyra and the remaining ones into planuloids. Scale: 0.6 mm.



Fig. 4. Ephyra (oral view) of *Linuche unguiculata*, two days after release from the strobila. Note the many zooxanthellae. (From photomicrograph). Abbreviations: cg = coronal groove, gf = gastric filament, r = rhopalium, z = zooxanthellae. Scale: 0.6 mm.

Scyphistomae, planuloids and ephyrae (Table 2) all had holotrichous isorhizas and heterotrichous microbasic euryletes nematocysts.

Discussion

Our original assumption was that the colonial coronates in São Sebastião Channel were *Linuche unguiculata*, considering the morphology and number of the internal cusps within the tube. The cup-shaped cusp is diagnostic of polyps of *L. unguiculata* (Leloup 1937, Ortiz-Corp's et al. 1987, Jarms 1991). Moreover, the size and proportions of the periderm tubes were within the ranges of *L. unguiculata* studied by Leloup (1937), Allwein (1968) and Ortiz-Corp's et al. (1987). The original descrip-

tion of the species was based on the medusa stage (Swartz 1788) and it is wise to study both stages in the life-cycle to make a precise identification (Jarms 1990, 1991). Werner (1979) was first to link the polyp stage of *Stephanoscyphus komaii* with the medusa *L. unguiculata*.

The lack of either ephyrae or medusae in plankton and suprabenthic faunal samples had been difficult to explain. Their absence was evidently due to the asexual reproductive modes employed locally—direct transformation of strobilating discs and segmentation originating planuloids, newly reported reproductive strategies for *L. unguiculata* and novelties for coronates. Arai (1997:166) defined strobilation as the process by which scyphistoma produces

Table 1.—Observations on 8 colonial scyphistomae of *Linuche unguiculata*. Abbreviations: St-e—length of period of strobilation (ds) originating ephyrae, St-p—length of period of strobilation (ds) originating planuloids, Se—length of period of segmentation (ds), E—ephyra development (ds), E/M—observations (ds) of ephyrae and medusa.

Scyphistoma (sample month)	1 (Jun 96)	2 (Mar 97)	3 (Mar 97)	4 (Mar 97)	5 (Mar 97)	6 (Mar 97)	7 (Mar 97)	8 (Apr 97)
St-e	3	2 and 1	—	—	—	—	1	2
St-p	7	8 and 1	—	—	7	—	5	7
Se	—	—	8	7	—	10	—	—
E	—	—	—	—	—	—	—	30
E/M	36	2 ^a and 38	—	—	—	—	27	54

^a The ephyra was preserved to study the cnidome.

ephyrae: “This requires disc formation (‘segmentation’) leading to fission, and also metamorphosis in which structures of the polyp are lost and replaced in each disc with those of the developing ephyrae.”

Therefore, the word segmentation in this work applies to the transverse fission of the scyphistoma, within an operculate tube, comparable with the strobilation in which all discs metamorphose into ephyrae. Wer-

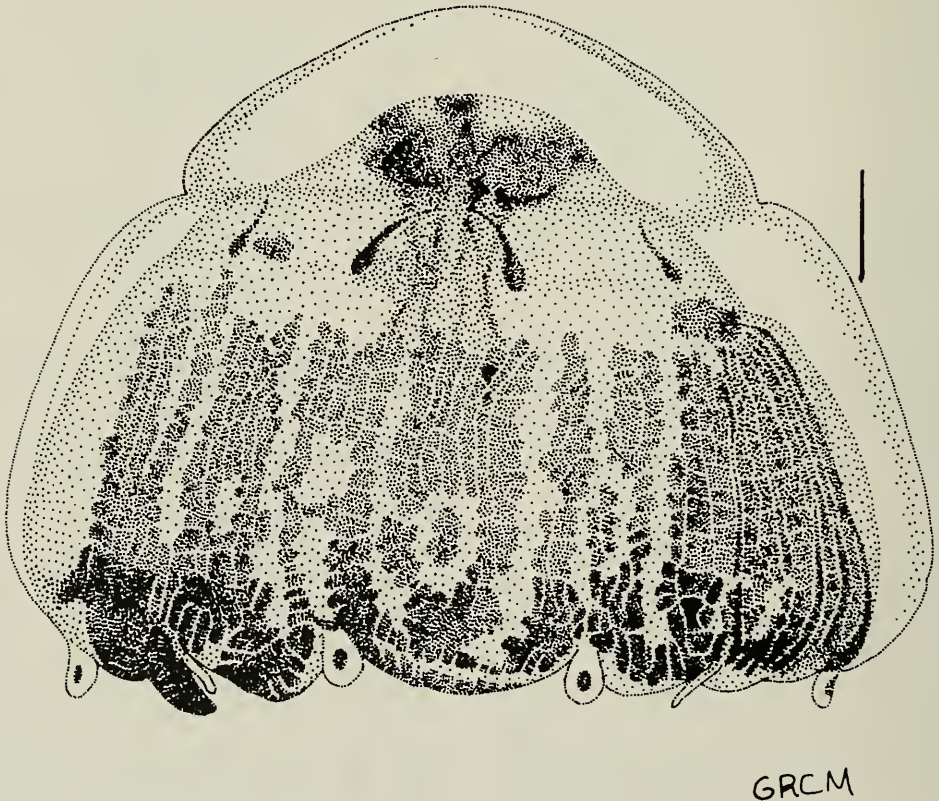


Fig. 5. Young medusa of *Linuche unguiculata*. The animal is shown in side view, to show the dark pattern due to the zooxanthellae in the gastrodermis and the arrangement of the paired gonads in cleft crescents. Note that the nearest lappet is enlarged as result of injury and later fusion of two original lappets. (From life and close-up VHS). Scale: 1 mm.

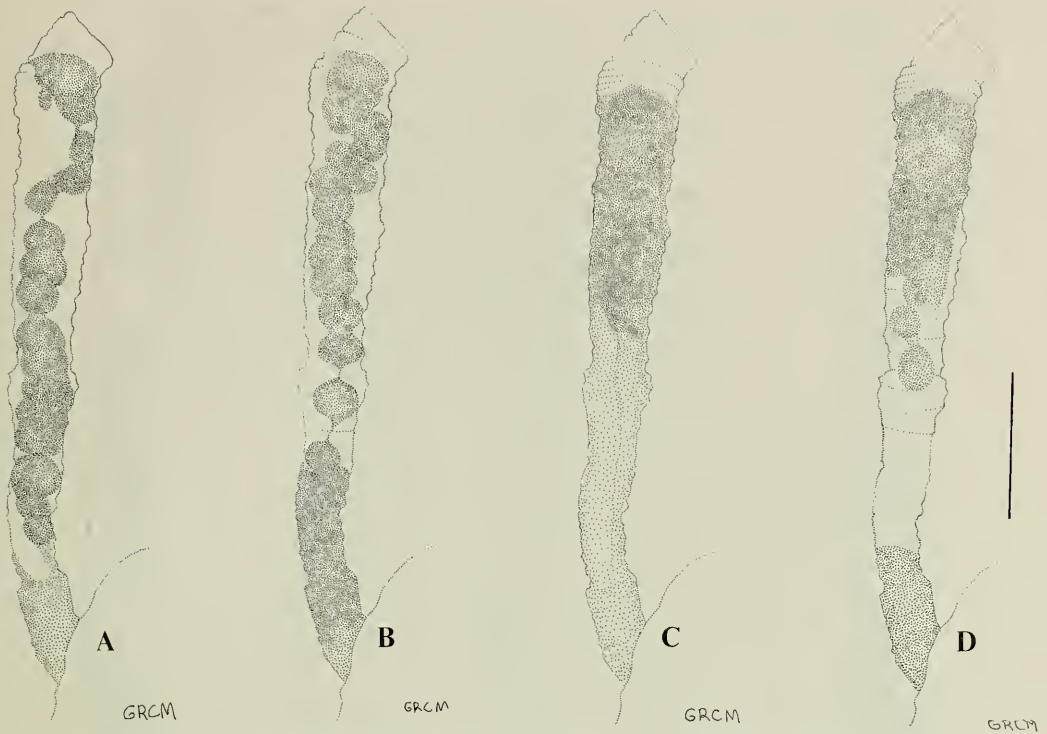


Fig. 6. Colony of *Linuche unguiculata* undergoing segmentation. A, planuloid formation (3.IV.97); B, planuloids almost distinct and the distal ones fused together (4.IV.97); C, regeneration of the column of the polyp starts by fusion of planuloids (dark areas) and the stretching of basal tissues (9.IV.97); D, contraction of the basal tissues, upon stimulation with a forceps, showing that the distal planuloids are entirely fused together (9.IV.97). Scale: 1.25 mm.

ner (1973) reviewed the known variation of the operculum in the scyphistomae of Coronatae. The only paper with a thorough account of the strobilation of *L. unguiculata* is that of Ortiz-Corp's et al. (1987). They observed the process in Puerto Rico, at temperatures of 25–28°C (December–May) and 28–30°C (June–November), for 7 yr. They noted strobilation once a year, sometimes within an operculate tube, with the production of free-swimming ephyrae. Werner (1979) also accounted for the annual strobilation of *L. unguiculata* under laboratory conditions. Werner (1979:94) hypothesized that for the colonial coronates “. . . their strobilation activities are genetically fixed to one distinct short season.” He argued that the surplus of energy stored by the polyps is available for colony growth,

in place of consecutive strobilation within one year the way solitary coronates are likely to do.

Jarms (1997) reported shortened life cycles of five species of Coronatae, the transformation of free ephyrae into planuloids and these into new polyps, due to unfavorable conditions of salinity, temperature or food supply. Planuloid formation by transformation of free ephyrae within the tube is known in the solitary *Nausithoe planulophora* (Werner 1971, Werner & Hentschel 1983, Jarms 1997) and *N. aurea* (Silveira & Morandini 1997), and by parthenogenesis in *Thecoscyphus zibrowii* (Werner 1984). A unique feature we have observed is the differing destiny of discs from the same strobila—one ephyra and many planuloids—with differing regulative mecha-

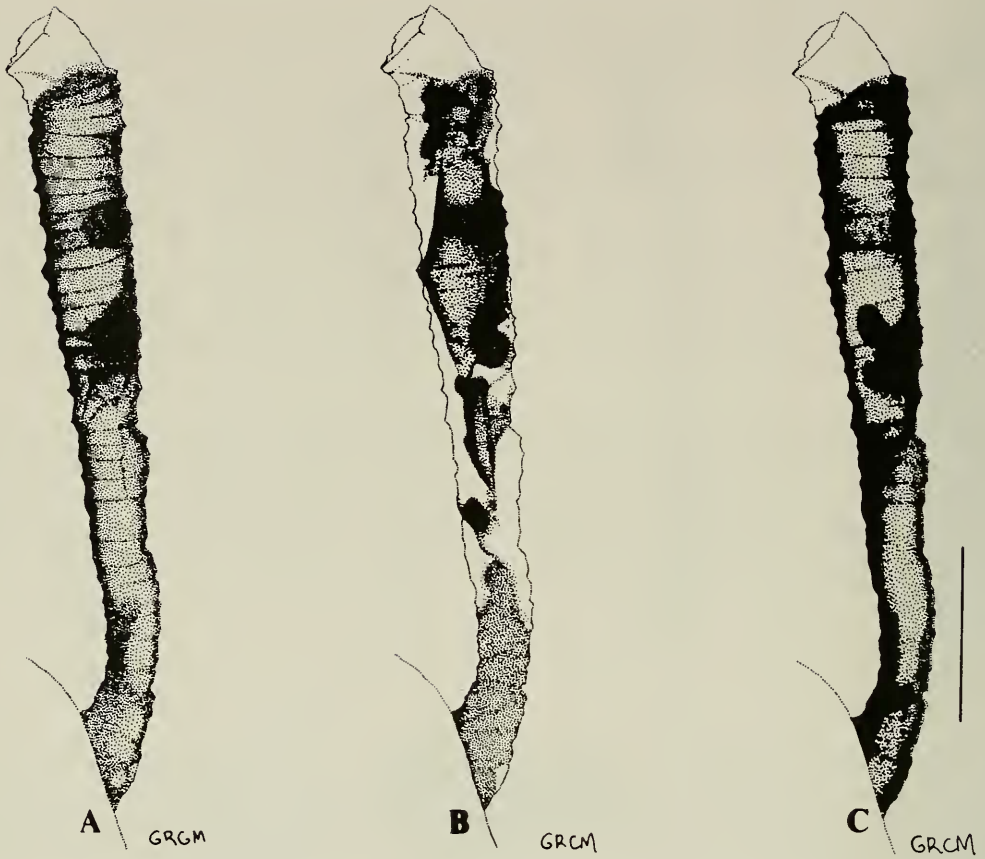


Fig. 7. Colony of *Linuche unguiculata* undergoing segmentation. A, the column of the polyp is almost entirely regenerated (13.IV.97); B, contraction of the tissues, upon stimulation with a forceps, to show that there is integration between the regenerated pieces, but that the column as a whole does not contract (13.IV.97); C, column totally regenerated, but the dark areas indicate the remains of fusing planuloids (14.IV.97). Scale: 1.25 mm.

nisms for each developing structure. Following the reasoning of Jarms (1997:275) on planuloid formation by *N. planulophora*, we believe the planuloids of *L. unguiculata* must be an alternative dispersive stage, since we have observed settlement and development of two new colonies. We hypothesize that segmentation is an advanced trait derived from the peculiar strobilation, with the addition of the operculum, perhaps the most derived response to the regulation of asexual reproduction in the species. *L. unguiculata* is a warm-water species (Mayer 1910, Kramp 1961, Ortiz-Corp's et al. 1987), and we have observed a new reproductive mechanism of the species to adapt

to a subtropical area in which there is a marked influence of both warm and cold water masses (see Campaner 1985). The absence of ephyra and medusa from plankton and suprabenthic samples is thereby explained.

The ephyrae (Fig. 4) and the young medusa (Fig. 5) closely resemble the descriptions of the adult medusa of *L. unguiculata* (Mayer 1910, Ortiz-Corp's et al. 1987). The medusa illustrated in the present paper resembles the developmental stage that Mayer (1910:559) described "that the gonads appear when the medusa is about 5 mm wide." The arrangement of the gonads and the shape and coloration of the umbrella are

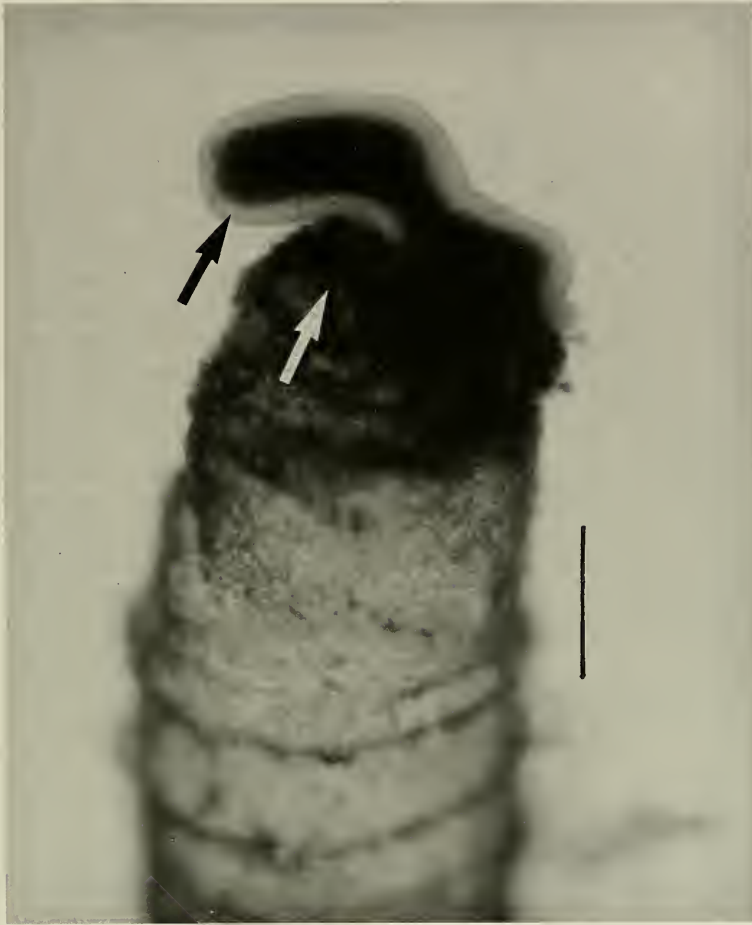


Fig. 8. Photomicrograph of the scyphistoma periderm tube of *Linuche unguiculata*, distal end and with operculum (white arrow). Note that one planuloid (black arrow) has emerged and rests upon the operculum. Scale: 0.3 mm.

Table 2.—Measurements of cnidae of cnidome of *Linuche unguiculata*. The range was taken from 20 nematocysts of each type at each stage, except the underlined measurements taken from only 9 nematocysts.

	Holotrichous isorhiza (μm)	Heterotrichous microbasic eurytele (μm)
Scyphistoma	10-6 \times 6-4	17-14 \times 14-11 <u>13-07 \times 10-05</u>
Ephyra	7-5 \times 4	15-14 \times 14-12 13-09 \times 12-08
Planuloid	7-6 \times 5-4	17-14 \times 14-12 13-09 \times 12-07

diagnostic for the species. The difficulty of obtaining the strobilae and the ephyrae-medusae reflects the prevailing asexual reproduction. The cnidome of scyphistoma, ephyra and planuloid are the same as recorded by Calder (1974) and Ortiz-Corp's et al. (1987) in medusae of *L. unguiculata*. The differences between our data may result from comparing different stages for the species. We followed Calder (1974) in separating the heterotrichous microbasic eurytele nematocysts into two size-classes, though they are almost one continuous size class.

There are some indirect indications, ei-

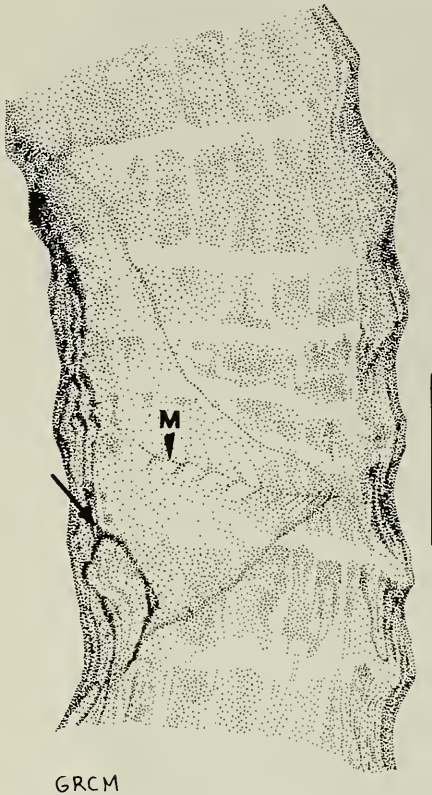


Fig. 9. Segment of periderm tube of *Linuche unguiculata* showing an internal cusp (since some had 2–3). Arrow points to the base of the outline of the cusp. Note that at the broad round margin (M) there are ridges. Scale: 0.3 mm.

ther in the swarming of the medusa (Larson 1982, Ortiz-Corp's et al. 1987, Halstead 1988), as well as in the outbreaks of their planulae (Russell & Tomchik 1993, Black et al. 1994), that in nature *L. unguiculata* strobilates seasonally (winter–spring) and the adult medusae occur in spring and early summer in the Caribbean, Atlantic coast of

Florida, and the Bahamas. Although some authors report concentrations of medusae of *L. unguiculata* (Table 3), only two medical incidents (dermatitis) linked with the medusae of this species have been reported in the literature (Penner 1962). Black et al. (1994) associated seabather's eruption—SBE—with planulae of *L. unguiculata* in Florida. Russell & Tomchik (1993) and Black et al. (1994) summarized outbreaks of SBE in Florida. They argued that there may be an interval of up to 25 yr, between major outbreaks. Nevertheless, Williamson et al. (1996:308–310) stated that the dermatitis SBE, besides having other names, is caused by different organisms in distinct regions. We hypothesize that *L. unguiculata* is a species with a long life-cycle mainly resulting from the long duration of the scyphistoma stage. Under variable conditions, this warm-water species may present an efficient colonizing ability by the scyphistoma that undergoes asexual reproduction and propagation.

The oral disc regression-regeneration process we observed in operculate scyphistomae on many occasions has never been reported in any coronate. This mechanism may be considered analogous to observations on some leptolid polyps, e.g., *Thyrosocyphus marginatus* (Harris 1990, and see revision in Crowell 1991). Tardent (1963) hypothesized that a regression-regeneration cycle in the hydranths of colonial leptolids would be a natural histophysiological rejuvenation mechanism for the colony, by extension a possible pattern for some species to secure perennation (*sensu* Cornelius 1992) in specific habitats. Nevertheless, it

Table 3.—Occurrence of swarms of medusae of *Linuche unguiculata* in Florida, the Caribbean and the Bahamas, from different sources.

Occurrence	Date	Author
Miami (Florida)	April 1950	Penner 1962
Sarasota (Florida)	July 1954	Penner 1962
Boca Grande (Florida)	July 1955	Penner 1962
Carrie Bow Cay (Belize)	Mar/Apr 1987; April 1988; Mar/Apr 1990	Larson 1992
The Bahamas	April/May 1989	Montgomery & Kremer 1995

remains an open question whether this process in laboratory observations really occurs under natural conditions (see revision in Hughes 1987).

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